A revision of the eggshell fragment of *Spheroolithus megadermus* from Laiyang, Shandong Province, China

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Abstract In 1958, a special type of dinosaur egg was discovered in Zhaotuan, Laiyang, Shandong Province, China. Although only a large eggshell fragment was collected, its extremely large thickness indicated that the eggshell fragment represented a new ootaxon. In previous studies, it was named *Spheroolithus megadermus* and assigned to the oogenus *Spheroolithus* under the oofamily of the Spheroolithidae based on the microstructure in radial view. However, a comparative study of the microstructure in tangential views between the large eggshell fragment from Laiyang and the recently reported *Multifissoolithus* from Zhejiang Province, China and Yamaguchi, Japan revealed that all of them have roughly paralleled and wavy clefts. Therefore, this study reassigned the large eggshell fragment from Laiyang to *Multifissoolithus* of the Dongyangoolithidae and discussed its unique compact layer near the eggshell's inner surface, as well as the chronological and spatial distribution of dongyangoolithid eggs. The reassignment of the holotype of *Spheroolithus megadermus* also indicates that the referred specimen of *Spheroolithus megadermus* from Changtu, Liaoning Province becomes the holotype of a new oospecies *Spheroolithus quantouensis*.

Key words Laiyang, Shandong; *Spheroolithus*; *Multifissoolithus*; dongyangoolithid eggs

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1 Introduction

Young (1959) described a large eggshell fragment collected in the middle part of Wangshi Group from Zhaotuan, Laiyang, Shandong Province. Due to its extremely large thickness of 5–7 mm, it was named *Oölithes megadermus*, which means a fossil egg with a thick eggshell (Young, 1959). In a review of the spherical dinosaur eggs from Laiyang, Shandong Province, Zhao and Jiang (1974) compared *O. megadermus* with other specimens and confirmed that it represented an independent oospecies. Zhao (1979) erected the Spheroolithidae based on the spherical dinosaur eggs from Laiyang. The large eggshell fragment was assigned to the

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type oogenus *Spheroolithus* of the Spheroolithidae. However, this assignment was uncertain due to the lack of comparative material (Zhao, 1979; Zhao et al., 2015). In a reassessment of the spherical dinosaur eggs housed at the Dalian Natural History Museum (DLNHM) from Changtu, Liaoning Province, Liu et al. (2013) described a half spherical egg with an eggshell thickness of 4.8–5.2 mm and considered it as a referred specimen of *Spheroolithus megadermus*.

Recently, a new type of dinosaur egg, *Multifissoolithus* was reported in Yiwu, Zhejiang Province, China and Shimonoseki, Yamaguchi, Japan, including two oospecies *M. chianensis* and *M. shimonosekiensis*. The eggshell of *Multifissoolithus* is 3.21–4.70 mm thick, with roughly paralleled and wavy clefts on the outer surface (Zhang et al., 2019; Imai et al., 2020). This ootaxon shared several characteristics with *Spheroolithus* such as a relatively thick eggshell and isolated eggshell units with triangular cunei near the inner surface of eggshell, but the clefts throughout the whole eggshell were not seen in *Spheroolithus* (Zhang et al., 2019). In this study, the eggshell microstructure in the tangential section of the large eggshell fragment from Laiyang, Shandong Province was studied for the first time, revealing the microstructural similarity between the large eggshell fragment from Laiyang and the *Multifissoolithus* fragment from Yiwu. Thus, the large eggshell fragment from Laiyang was reassigned to *Multifissoolithus*, and a new oospecies of *Spheroolithus* was erected based on the specimen from Changtu, Liaoning Province which indeed belongs to *Spheroolithus*. The revision of the large eggshell fragment from Laiyang also extended the chronological and spatial distribution of dongyangoolithid eggs.

2 Material and methods

A small piece of eggshell fragment was cut from the large eggshell fragment (IVPP V 2337) from Laiyang, Shandong Province and afterwards was embedded in EXAKT Technovit 7200 one-component resin. The eggshell fragment was cut radially and tangentially using an EXAKT 300CP cutting system. The thin sections were grinded and polished to the thickness of about 50 μm using an EXAKT 400CS variable speed grinding system with P500 and P4000 abrasive papers. The thin sections were observed and photographed under normal and polarized lights using a Zeiss Axio Imager A2 polarized light microscope. The large eggshell fragment and the thin sections were catalogued at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP).

3 Systematic paleontology

Dongyangoolithidae Zhang et al., 2019

Revised diagnosis Spherical to oval eggs, smooth outer surface with clefts and round pores, eggshell unit assemblages separated by large cavities in radial sections, a compact layer composed of cones near the inner surface of eggshell.

***Multifissoolithus* Zhang et al., 2019**

Revised diagnosis Eggs with a diameter of 8–10 cm randomly arranged in nest, eggshell 3.21–5.70 mm thick composed of cone-shaped or columnar eggshell unit assemblages, roughly paralleled and wavy clefts on the outer surface connecting to the large cavities between eggshell unit assemblages in the inner portion of the eggshell. Horizontal accretion lines throughout the whole eggshell.

***Multifissoolithus megadermus* (Young, 1959) comb. nov.**

(Figs. 1–4)

Oölithes megadermus Young, 1959, p. 34–35; Zhao and Jiang, 1974, p. 66, pl. 4: 8

?*Spheroolithus megadermus* Zhao, 1979, p. 332; Wang et al., 2012, fig. 6

Spheroolithus megadermus Zhao et al., 2013, p. 4665, fig. 2; Zhao et al., 2015, p. 67, figs. 44A, 45

Holotype A large eggshell fragment (IVPP V 2337).

Locality and horizon Zhaotuan, Laiyang, Shandong Province, Upper Cretaceous Jiangjunding Formation.

Revised diagnosis Eggshell 5.7 mm thick composed of cone-shaped eggshell unit assemblages, secondary eggshell units in the large cavities between eggshell unit assemblages and the clefts and pores on outer surface.

Description After removing the red sandstones on the outer surface of the large eggshell fragment, roughly paralleled and wavy clefts can be observed clearly with the naked eye (Figs. 1, 2). The eggshell fragment is 5.7 mm in thickness. In radial views, horizontal accretion lines are distributed evenly throughout the whole eggshell. The cones form a dark compact layer with a light stripe and distinct radial microstructure near the inner surface of the eggshell. There are large cavities above the compact layer. A few cone-shaped eggshell unit assemblages extended to the outer surface of the eggshell from the compact layer. Near the outer surface, adjacent eggshell unit assemblages fuse together (Fig. 3A, B). Meanwhile, secondary eggshell units are distributed randomly in the clefts between the eggshell unit assemblages and block some of the round pore

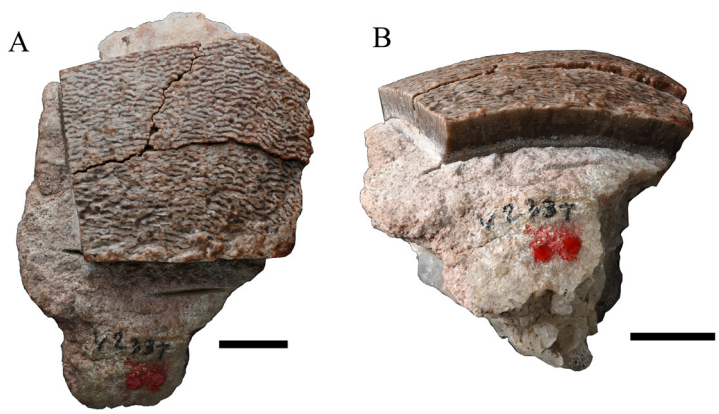

Fig. 1 Top (A) and lateral (B) views of the large eggshell fragment (IVPP V 2337) from Laiyang, Shandong Province
Scale bars equal 1 cm

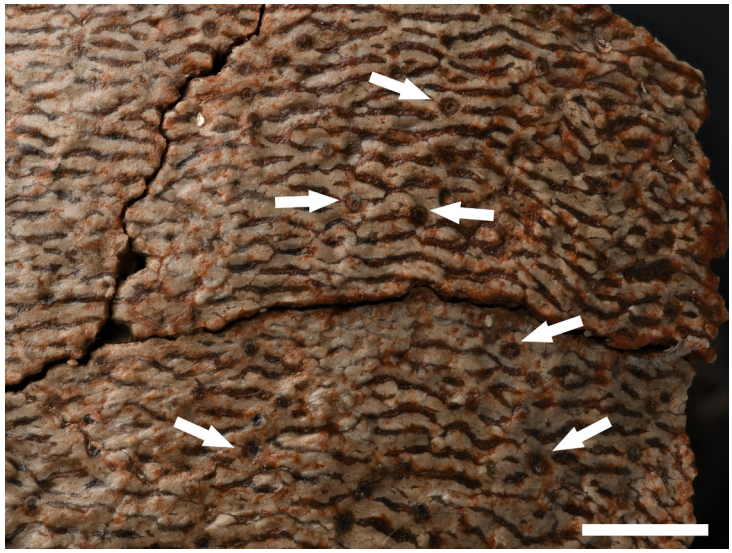

Fig. 2 Enlargement of the roughly paralleled and wavy clefts and the round pores (white arrows) on the outer surface of IVPP V 2337
Scale bar equals 0.5 cm

openings on the outer surface (Figs. 3C, 4A–C). In tangential views, the clefts become wider gradually towards the inner surface of the eggshell (Fig. 4A–C). Near the inner surface of the eggshell, polygonal eggshell units were separated by large cavities (Fig. 4D–F). Also, in the tangential view through the dark compact layer, all eggshell units are fused extensively with clear boundaries between each other. Only a few round and elongated pores were visible (Fig. 4G, H).

Comparison The large eggshell fragment can be easily assigned to *Multifissoolithus* of Dongyangoolithidae instead of *Spheroolithus* of Spheroolithidae based on the roughly paralleled and wavy clefts on the outer surface, as well as the tangential sections through the outer portion (Figs. 1, 2, 4A–C). By contrast, the eggshell units are fused extensively in the outer portion of the eggshells of *Spheroolithus*, with only irregular cavities left between the eggshell units (Zhao and Jiang, 1974; Liu et al., 2013; Zhao et al., 2015; Zhu et al., 2021). Although the microstructure of the eggshell is similar to the other oospecies of *Multifissoolithus*, its extreme thickness significantly exceeds that of all known *Multifissoolithus* eggs (Zhang et al., 2019; Imai, 2020). Thus, a new combination *M. megadermus* is erected based on the large eggshell fragment.

Spheroolithidae Zhao, 1979

Spheroolithus Zhao, 1979

Revised diagnosis Spherical to subspherical eggs with 74–99 mm in length, eggshell 2.2–5.5 mm in thickness, cone-shaped eggshell unit assemblages separated by large cavities in the inner portion of eggshell, fusing extensively in the outer portion of eggshell, irregular cavities between eggshell units in the outer portion of eggshell, slender or branched eggshell units separated from each other near the outer surface of eggshell.

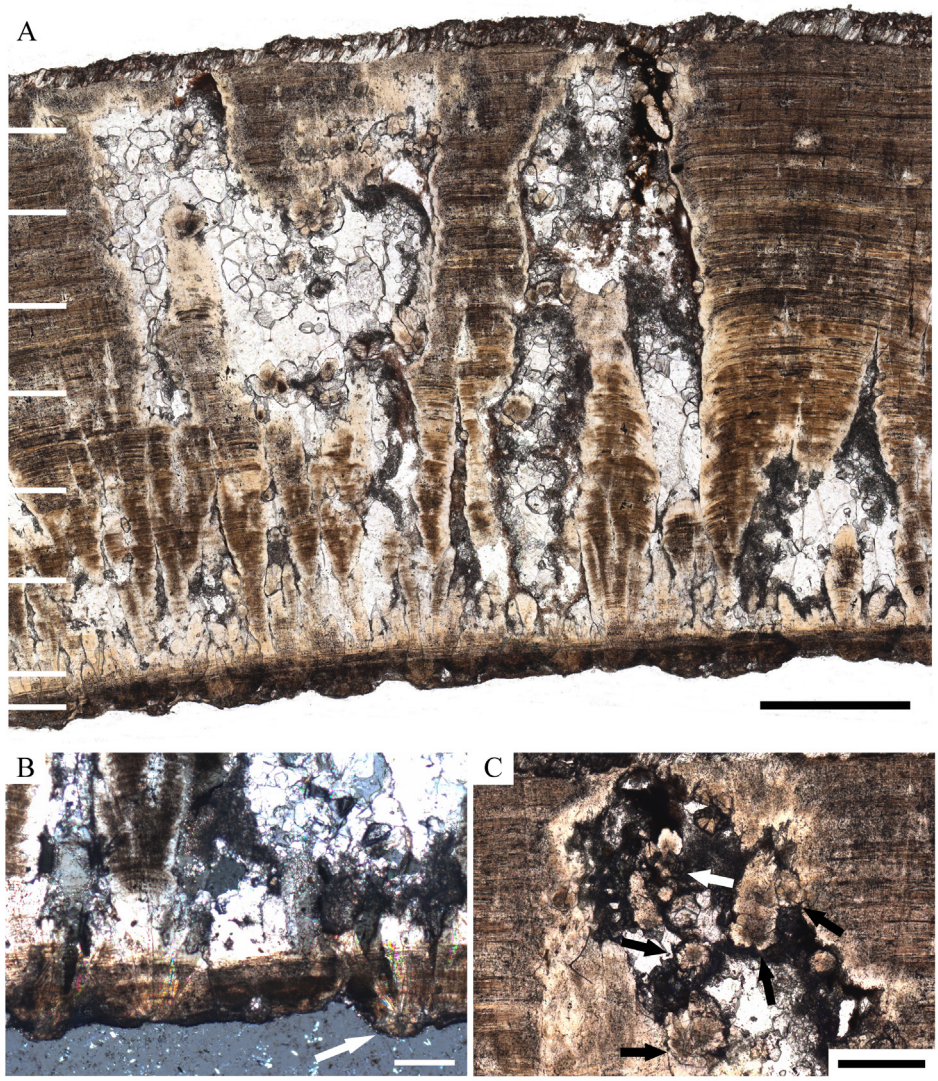

Fig. 3 Eggshell microstructure of radial sections of *Multifissoolithus megadermus* comb. nov. (IVPP V 2337) A. radial section parallel to the clefts; lines at the left side indicate rough positions of fig. 4A–H in ascending order; B. enlargement of the dark compact layer near the inner surface of eggshell under polarized light, showing the radial microstructures of the cones; nucleation center is indicated by the white arrow; C. secondary eggshell units in the cleft between eggshell assemblages near the outer surface of eggshell (black and white arrows). Scale bars equal 1 mm in A, 0.5 mm in B and 0.4 mm in C

***Spheroolithus quantouensis* oosp. nov.**

(Liu et al., 2013:figs. 6–8)

Etymology "quantou" refers Quantou Town, the locality where the specimen was collected.

Holotype A half egg with secondary calcite crystals inside (DLNHM D154).

Locality and horizon 1 km southwest of Quantou Railway Station, Changtu, Liaoning

Province, Upper Cretaceous, upper portion of the second member of the Quantou Formation (Liu et al., 2013).

Diagnosis Spherical egg with 9.0×8.0 cm in size, eggshell 4.8–5.5 mm thick with dark strips in the middle portion and horizontal dark lines in the outer portion.

Comparison This specimen is very similar to *Spheroolithus spheroids* and *S. chiangchiungtingensis* except for the following features: the eggshell is much thicker those that of *S. spheroids* (2.4–3.2 mm, Liu et al., 2013) and *S. chiangchiungtingensis* (2.20 mm,

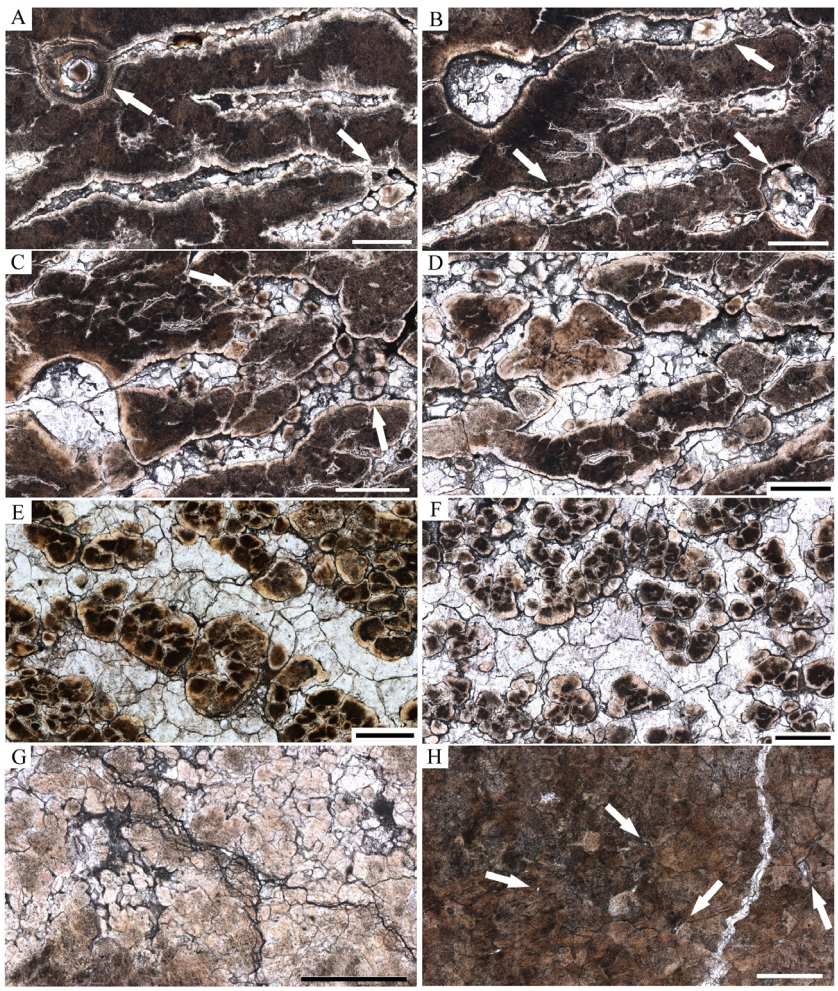

Fig. 4 Eggshell microstructure of tangential sections of *Multifissoolithus megadermus* comb. nov. (IVPP V 2337)

A–C. through the outer portion of eggshell, the white arrows indicate the secondary eggshell units in the clefts and pores; D–F. through the inner portion of eggshell, showing the wavy eggshell units assemblages gradually split into isolated eggshell units; G, H. through the dark compact layer near the inner surface of eggshell, the white arrows in H indicate round and elongated pores

Scale bars equal 0.5 mm

Zhao et al., 2015); in the outer portion of the eggshell, the eggshell units have more branches and lower density of horizontal dark lines than *S. spheroids* and *S. chiangchiungtingensis.*

4 Discussion

Spheroolithus was first reported in Laiyang, Shandong Province, China, including two oospecies *S. chiangchiungtingensis* and ?*S. megadermus* (Zhao, 1979). In subsequent studies, *Spheroolithus* eggs were reported in Liaoning Province, China, Mongolia, Kazakhstan, Spain, U.S.A. and Canada (Hirsch and Quinn, 1990; Mikhailov, 1991, 1994, 1997; Zelenitsky and Hills, 1997; Bray and Hirsch, 1998; Lucas et al., 2012; Liu et al., 2013; Sellés et al., 2014), but all of them were reassigned to *Stromatoolithus* based on their ornamentation, pore canals and accretion lines except for those from Liaoning Province, China (Zhu et al., 2021). Thus, the distribution of *Spheroolithus* was restricted to the Shandong and Liaoning provinces in China. In recent studies, *S. chiangchiungtingensis* was split into two oospecies, including *S. spheroids* and *S. chiangchiungtingensis*, whose holotypes were IVPP V 730 and IVPP RV 74002 (field number G5547), respectively (Zhao et al., 2013, 2015). ?*Spheroolithus megadermus* became an undoubted oospecies in *Spheroolithus* based on the similarity between the large eggshell fragment from Laiyang, Shandong Province (IVPP V 2337) and the half egg studied in detail from Changtu, Liaoning Province (DLNHM D154) (Liu et al., 2013; Zhao et al., 2015). It is noteworthy to mention that this comparative study was merely based on the radial eggshell microstructure of V 2337 and DLNHM D154. The tangential eggshell microstructure of V 2337 was previously unknown due to the lack of tangential thin sections. Thus, the misassignment of V 2337 highlights the importance of the tangential eggshell microstructure in dinosaur egg identification.

As described in the above, the features of the tangential microstructure in the outer portion clearly showed that V 2337 belongs to *Multifissoolithus*. On the other hand, the compact layer composed of the cones with radial microstructure was first noticed in dongyangoolithid eggs (Fig. 3A, B). This layer was also visible in the eggshells of *M. chianensis* and *M. shimonosekiensis*, due to the fact their inner surface was not weathered (Zhang et al., 2019:fig. 3A, B; Imai et al., 2020:fig. 4), and possibly seen in the eggshell of *Dongyangoolithus nanmaensis* despite the weathering of inner surface (Jin, 2013:pl. X2, 3). However, this layer was not observed in *Spheroolithus*. In comparison with the large cavities in the inner portion of the eggshell, there were very few pores in this compact layer (Fig. 4H). Due to the large cavities connected to the clefts on the outer surface, the gas conductance for most portions of dongyangoolithid eggshells would be relatively high. The compact layer near the inner surface could be the main conductive barrier of water vapor and respiratory gases. By contrast, either the middle or outer portion of the eggshells of other oofamilies has the lowest pore density (Zhao et al., 2015).

At present, dongyangoolithid eggs were reported in Zhejiang and Shandong provinces

in China, Yamaguchi in Japan and the Sihwa Basin in South Korea (Kim et al., 2009; Zhang et al., 2019; Imai et al., 2020). *Multifissoolithus chianensis* from Yiwu and *M. megadermus* from Laiyang occur in the Lower Cretaceous Chaochuan Formation (119–104 Ma, Aptian–Albian) and the Upper Cretaceous Jiangjunding Formation, respectively (Zhao et al., 2013; Zhang et al., 2019). *Multifissoolithus shimonosekiensis* from Yamaguchi occurs in the Shimonoseki Subgroup (Aptian–Albian, Imai et al., 2020). The dongyangoolithid eggs from the Sihwa Basin occur in the Lower Cretaceous Sihwa Formation (119.8±2.3 Ma, 118.6±2.3 Ma and 125.5±2.4 Ma, Aptian, Kim et al., 2009). The geological ages of the Chaochuan and Sihwa formations, and the Shimonoseki Subgroup suggested that the dongyangoolithid eggs from Zhejiang Province in China, Yamaguchi in Japan and the Sihwa Basin in South Korea are almost contemporary, representing the earliest record of dongyangoolithid eggs in East Asia. The isotopic dating of the Jiangjunding Formation in Laiyang is still unknown. Although the lithologically similar Hongtuya Formation in Jiaozhou can be dated to 73.5±0.3 Ma (Campanian, Yan et al., 2003; Yan and Chen, 2005; Zhang et al., 2008), the hadrosaurine *Tanius sinensis* from the same horizon of *M. megadermus* suggest that the geological age of the Jiangjunding Formation is Coniacian–Santonian (Hu et al., 2001). Due to the absence of dongyangoolithid eggs in the overlaying Jingangkou Formation in Laiyang and other younger Upper Cretaceous deposits in China (Hu et al., 2001; Wang et al., 2012; Zhao et al., 2013), the *M. megadermus* could represent the latest member for Dongyangoolithidae.

5 Conclusions

(1) The study of the tangential sections of the "*Spheroolithus megardermus*" from Laiyang, Shandong Province suggested that this large eggshell fragment belongs to *Multifissoolithus* rather than *Spheroolithus*. Due to its extremely thick eggshell, it now represents a new combination *Multifissoolithus megardermus*. The half egg housed at DLNHM represents a new oospecies *S. quantouensis.*

(2) The compact layer near the inner surface of dongyangoolithid eggshells is the main conductive barrier of water vapor and respiratory gases.

(3) Dongyangoolithid eggs are currently reported in China, Japan and South Korea and their temporal presence ranges from the Aptian to Santonian in the Cretaceous.

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对产自山东莱阳的厚皮圆形蛋碎蛋壳的修订

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摘要：1958年在山东莱阳赵疃村发现了一种特殊类型的恐龙蛋化石。尽管只发现了一枚较大的蛋壳碎片，但其极大的厚度表明它是一个新的蛋种。研究者根据蛋壳径切面的显微结构将它归入圆形蛋科的圆形蛋属并命名为厚皮圆形蛋。然而，与新近报道的产自中国浙江省和日本山口县的多裂隙蛋属的弦切面结构进行对比发现，它们都具有大致平行并且呈波浪状的裂隙。因此将产自莱阳的这块蛋壳碎片重新归入东阳蛋科的多裂隙蛋属，并讨论了东阳蛋类近蛋壳内表面的致密层以及东阳蛋类的时空分布情况。同时，产自辽宁昌图的厚皮圆形蛋的归入标本成为新修订的泉头圆形蛋的正型标本。

关键词：山东莱阳，圆形蛋属，多裂隙蛋属，东阳蛋类

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